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Cambridge, Mass. November 6, 1972 Number 397

XYLOREDO, A NEW TEREDINID-LIKE ABYSSAL WOOD-BORER (MOLLUSCA, PHOLADIDAE, XYLOPHAGAINAE)

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Abstract. *Xyloredo*, a new genus of Xylophagainae characterized by having a long burrow with a calcareous lining, is described. Three new species belonging to this genus are also described, *Xyloredo nooi* and *X. ingolfia* from the Atlantic and *X. naceli* from the Pacific. The systematic position of the genus, its superficial resemblance to the Teredinidae, and the factors controlling the distribution of the species are discussed.

INTRODUCTION

The Xylophagainae are benthic, mainly deep-sea wood-borers. Their distribution is dependent on the presence of woody plant material and their dispersal on the free-swimming larval stage. From available evidence it appears that wood in the deep sea is scarce and its distribution patchy. Bruun (1959) reported on the remnants of plant material collected by the R/V GALATHEA during a circumnavigation of the globe. J. Knudsen (1961) reported on the *Xylophaga* collected on that cruise and also discussed the presence of plant debris in the deep sea, summarizing the results of earlier expeditions. An analysis of the data in these reports shows that 56 of the 180 successful bottom stations made by the GALATHEA in depths between 400 and 7290 meters yielded plant material. Only 22 of these hauls had woody material of sufficient size (e.g., over 10 grams) to support borers, but species of *Xylophaga* were taken at only 11 stations.

On the basis of material now available, the ranges of many of the species in this subfamily appear to be limited. The known ranges may be a reflection of the limited number of dredging stations but may also be because 1) the dispersal efficiency of the larvae is poor (J. Knudsen, 1961) and 2) wood in the deep sea is not only scarce but is found in "islands" of plant debris, usually in deep trenches near land, particularly in the regions of large rivers (Bruun, 1959). In order to better understand the distribution of these borers, we need to know more about their life history, particularly the length of time the larvae spend in the plankton and their behavior at the time of settlement.

Most *Xylophaga* are obtained by dredging, though a few species occurring in high latitudes can be found in shallow water, some even just subtidally in old wrecks or piling (Tomlin, 1920; Dons, 1929a, 1929b, 1940). In 1961 H. Turner attached a series of wood panels to the mooring line of a buoy set out by the Woods Hole Oceanographic Institution at 39°30′N; 69°40′W (on the Gay Head, Martha's Vineyard-Bermuda transect) in 3000 meters. When the panels were retrieved in October 1961, the bottom one was found to have been heavily attacked by *Xylophaga* (approximately 100 per square centimeter). This was the first time that "new" wood had been submerged to such a depth sufficiently rapidly so that there was no possibility of the larvae settling on the way down. Unfortunately, the specimens were too young for positive identification and no additional panels have been exposed at this site. About the same time the United States Navy began testing the performance of various materials, including wood, in the deep sea (DePalma, 1969; Muraoka, 1964–1967). These tests at depths of 1000 to 2000 meters have added greatly to our knowledge of the Xylophagainae and resulted in the discovery of a new genus, represented by three new species. Species in this new genus (*Xyloredo*, p. 3) are remarkably close to the teredinids in superficial appearance, as they produce long, often tortuous tunnels which have a calcareous lining; the valves, as in all Xylophagainae, are teredinid-like. The lack of pallets for closing the burrow and of apophyses for the attachment of the foot muscle, and the presence of a mesoplax, definitely place them in the Pholadidae, subfamily Xylophagainae.

Though mentioned in the literature (R. Turner, 1966a, 1969), this new genus was not named or described. Specimens of *Xyloredo nooi* (p. 5), the first new species to be received, were taken from tests put out by the U. S. Naval Oceanographic Office in the Tongue of the Ocean, Bahama Islands, in 1737 meters (DePalma, 1969). At this site, panels set in contact with the bottom were completely riddled, while those 15 meters off the bottom were entirely free of borers. Wood panels submerged by the U. S. Naval Civil Engineering Laboratory south of San Miguel Island off Port Hueneme, California, in 2072.6

meters were the source of the second new species, *Xyloredo naceli* (p. 9). At this site, panels 15 centimeters off the bottom were much more severely attacked by two species of xylophagaids than those only one meter up on the rack (Muraoka, 1966b). Tipper (1968), working with *Xylophaga washingtona* Bartsch off the Oregon coast, found that the number of borer penetrations dropped most markedly within the first 6 centimeters above the bottom. These findings suggest that the larvae probably remain close to the bottom throughout their free-swimming stage and that, except in areas where there are strong bottom currents, they probably are not widely dispersed (R. Turner, 1966b, 1968).

Xyloredo ingolfia (p. 7), the third new species belonging to this genus, came from a piece of wood dredged in 1896 by the INGOLF Expedition south of Eyrabakki, Iceland, from 1783 meters. This species appears to be more closely related to the California species than to the one from the Tongue of the Ocean.

As with many species of molluscan wood-borers, it is difficult to determine which characters of the species of *Xyloredo* will prove most stable and useful for taxonomic purposes until large series from several localities, representing all growth stages, are available for study. As intimated above, wood-borers from great depths are difficult to obtain, and such series may not be available for many years. In fact, the publication of the taxa included in this report has been delayed for five years while efforts were made to obtain additional material. Hopefully, knowledge of the existence of these remarkable Xylophagainae will stimulate personnel on dredging cruises and deep submersible dives to collect and preserve woody plant material. In addition to borers, dredged wood is a rich source of many species of benthic invertebrates.

Xyloredo[1], new genus

Type species. *Xyloredo nooi* Turner, new species.

Description. Valves typical of subfamily Xylophagainae and virtually indistinguishable from valves of *Xylophaga*; apophyses lacking; chondrophore, internal ligament, umbonal-ventral sulcus and ridge, and ventral condyle well developed. Mesoplax small, flat, triangular and only lightly calcified. Burrow, depending on size and age of specimen, 5 to 30 times length of valves. Posterior two-thirds of burrow with calcareous lining marked with distinct rings and covered by thin, outer periostracal layer which extends anteriorly as border (Plate 1, fig. 2). Periostracal covering of valves extending posteriorly as sheath that is continuous with heavy periostracal band on anterior end of tube. Mantle fold attached to anterior end of tube, point of addition of both periostracum and calcium. Burrow lining in very young specimens either entirely periostracal or lightly calcified.

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[1] A compound word, combining *Xylo-* from *Xylophaga* and *-redo* from *Teredo*, indicating the teredinid-like appearance of these Xylophagainae.

Combined incurrent and excurrent canals extend length of tube and attach to calcareous lining at anterior end of siphons. Siphons short, separate and apparently margined with few cirri.

Visceral mass similar to *Xylophaga* (Purchon, 1941; Turner and Johnson, 1971), contained completely between valves. Ctenidium of single demibranch nearly covering sides of visceral mass. Mouth broad and slitlike; labial palps inconspicuous. Esophagus short, wide, and flattened; stomach large, subglobular, with large crystalline style sac opening into it at posterior end. Style sac bent forward so that lower end protrudes slightly through visceral mass posteroventral to foot. Caecum large, U-shaped, and located mainly on the right side.

Remarks. The general description of the anatomy of *Xyloredo* given above was derived from a study of the remains of specimens of all three species. Unfortunately none was sufficiently well preserved for detailed dissection or sectioning.

Xyloredo differs from *Xylophaga* by having: 1) a long, teredinid-like burrow with a calcareous lining, 2) a thin periostracal sheath extending from the valves to the heavier periostracal border of the tube, and 3) extended incurrent and excurrent canals. The siphons of *Xyloredo* are short and separate, and when the animal is removed from its burrow it resembles a shipworm without its pallets.

Unlike the Teredinidae, *Xyloredo* has short, broad ctenidia, and all of the visceral mass is contained between the valves; a mesoplax is present but pallets and apophyses are lacking. In addition, the calcareous tube of *Xyloredo* is thin, regularly ringed, and covered externally with a shiny periostracum.

The superficial resemblance of *Xyloredo* to the Teredinidae is a result of convergence. The Xylophagainae are probably most closely related to the Jouannetinae, a subfamily of rockboring pholads, which also lack apophyses and have the pedal retractor muscle inserted in the typical bivalve position anterior to the posterior adductor muscle.

The discovery of this teredinid-like genus of Pholadidae necessitates a reexamination of fossil teredinids, especially those with ringed tubes. If valves are not present, or if the inner surface of the valves cannot be examined to ascertain whether apophyses are present, it may be impossible to distinguish fossil *Xyloredo* from the Teredinidae. It is, of course, possible that all fossil tubes with regular rings are *Xyloredo* or some closely related fossil genus. Many teredinid tubes are marked with rings, but not in the regular, evenly spaced fashion found in *Xyloredo*.

Fossil deposits produced in the deep sea are virtually unknown, so perhaps there is no need to be concerned about fossil *Xyloredo*. However, like *Neopilina*, it might well be that at one time their ancestors lived in shallower waters. It is possible that, as a result of competition with the more efficient Teredinidae, only the deep-water species survive.

Range. Species of *Xyloredo* are known in the Atlantic Ocean from off Iceland and from the Tongue of the Ocean, Bahama Islands. In the eastern Pacific they are known only from off San Miguel Island, near Port Hueneme, California. *Xyloredo* may well be world-wide in distribution in depths of over 1500 meters, but further dredging and testing are needed to prove this.

Xyloredo nooi[1], new species

Plates 1 and 2

Type locality. From test panels submerged in the Tongue of the Ocean (25°54′N; 77°49′W), off the north end of Andros Island, Bahama Islands, in 1737 meters, from 4 April 1962 to 17 February 1965 (DePalma, 1969).

Types. Holotype, Museum of Comparative Zoology 279631. Paratypes from the same and other panels exposed at the same locality, Museum of Comparative Zoology 279632, 279633, 279634, 279635, and the Universitetets Zoologiske Museum, Copenhagen.

Description. Shell globose, valves reaching 10 mm in length and 10.5 mm in height, thin, fragile; umbos prominent. Periostracum relatively thick, golden brown, glistening and covering entire valve. Beaked portion of anterior slope sculptured with numerous, finely denticulated ridges (24 ridges on holotype). Posterior portion of anterior slope narrow; ridges closely spaced, coarsely denticulated, usually thickened posteriorly and extending only about one-half distance to shallow umbonal-ventral sulcus. Disc sculptured with fine growth lines only. Posterior slope high, reflected near dorsal margin and sculptured with fine growth lines. Umbonal reflection thin, wide and adhering closely to surface of valves posteriorly, free anteriorly.

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[1] An acronym based on the initials of the Navy Oceanographic Office, Washington, D.C., which was responsible for the tests in the Tongue of the Ocean, Bahama Islands, from which the specimens were obtained.

Inner surface of valves smooth and glistening. Umbonal-ventral ridge narrow, high, slightly to strongly segmented and not greatly enlarged at ventral condyle. Chondrophore and internal ligament prominent (Plate 2, fig. 5). Disc separated from posterior slope by pronounced groove extending from umbo to posterior ventral margin. Posterior adductor muscle scar large, elliptical, and divided; upper part (on reflected portion of posterior slope) with irregular impressions, lower part with chevron-shaped impressions. Anterior adductor muscle scar covering umbonal reflection. Siphonal retractor muscle scars not impressed. Pedal retractor muscle scar elongate, located about midway on anterior margin of posterior adductor muscle scar. Mesoplax small, consisting of two flat, broad, subtriangular plates lying on dorsal surface of anterior adductor muscle and composed largely of periostracum.

Burrow long, teredo-like, with thin, calcareous lining for about three-fourths its length. Tubular lining marked with distinct rings and covered with thin, yellow-brown periostracum which extends as border anteriorly (Plate 1, fig. 2). Portion of animal between valves and tube covered by smooth, golden-brown, periostracal sheath, continuous anteriorly with periostracum of valves and posteriorly with periostracal border of tube. Tubes of young specimens (up to 10 mm long) may be entirely periostracal. Burrow opening on surface of wood with white, slightly raised, often divided cone about 1 mm in diameter. Siphons short and separate. Protoconch unknown.

Valve measurements.	Length	Height	
	9.5 mm	10.0 mm	Holotype
	9.5	9.8	Paratype
	7.2	7.8	"
	6.7	6.9	"
	5.0	5.1	"

Remarks. This species is closely related to both *Xyloredo naceli* and *X. ingolfia* (see also *Remarks* under *ingolfia*). It differs from them in having a much thinner burrow lining, a high, reflected posterior slope on the valves, and a proportionately smaller, more highly placed and divided posterior adductor muscle scar. In addition, the periostracal sheath extending between the valves and the calcareous tube is smooth. On the basis of the material at hand, *nooi* appears to be a much larger species. Size in borers, however, is often not a reliable taxonomic character, and an understanding of the size range requires the examination of large series from varied substrata. Stenomorphic adults often result from over-crowding or from penetration of an unusually hard substance.

The panels from which specimens of *nooi* were removed had been in the water for over 2½ years and were so badly riddled that the white, calcareous tubes showed through the thin surface. The general appearance of the wood was the same as that of a panel riddled with teredinids. It was not until the borers were exposed and examined closely that their pholad affinities were recognized. Many of the specimens were dead and their burrows filled with mud, with only the calcareous tube and valves remaining.

Unfortunately, the panels were not preserved immediately upon removal from the water, so the borers were in poor condition. Therefore, little anatomical work could be done, though it was possible to determine that the visceral mass was contained between the valves and that there was a large, U-shaped, wood-storing caecum.

The bottom at the test site was a gray mud; the temperature was 4°C and the salinity 35 ‰ (DePalma, 1969).

Range and specimens examined. Known only from the type locality.

Xyloredo ingolfia[1], new species

Plates 3–5

Type locality. From wood dredged by the INGOLF Expedition at station 67, south of Eyrabakki, Iceland (61°30′N; 22°30′W), in 975 fathoms [1783 meters].

Types. Holotype, Museum of Comparative Zoology 279636. Paratypes from the same locality, Museum of Comparative

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[1] Named for the Danish INGOLF Expedition, which collected the wood from which the specimens were obtained.

Zoology 279637, and the Universitetets Zoologiske Museum, Copenhagen.

Description. Shell globose, valves reaching 2.5 mm in length and 2.0 mm in height, thin, fragile, with prominent umbos; thin, glistening, almost colorless periostracum covering disc and posterior slope. Beaked portion of anterior slope wide, extending more than one-half distance to ventral margin; sculptured with close-set and very finely denticulated ridges. Posterior portion of anterior slope about two-thirds width of beak, sculptured with close-set ridges which extend to very slightly impressed umbonal-ventral sulcus. Disc sculptured with well-marked growth lines. Posterior slope small, low and not clearly demarcated on outer surface of valve. Umbonal reflection thick, narrow, short and free except at posterior end.

Inner surface of valves smooth, slightly shiny to chalky (perhaps owing to long preservation). Umbonal-ventral ridge wide, flattened, often varying in width, irregularly segmented and not enlarged at ventral condyle. Chondrophore and internal ligament large. Disc not clearly separated from posterior slope. Posterior adductor muscle scar large, slightly raised, elliptical, extending nearly to ventral margin, with irregular, transverse impressions. Anterior adductor muscle scar covering umbonal reflection. Siphonal retractor muscle scars not impressed. Pedal retractor muscle scar small, elongate to oval and located just anterior to posterior adductor muscle scar. Mesoplax of two very small, narrow, subrectangular, flat, calcified plates lying on dorsal surface of anterior adductor muscle.

Burrow 10 to 15 times length of valves; calcareous tubular lining three-fourths length of burrow. Tube relatively heavy, marked with uniform, close-set, raised rings, and covered with light tan periostracum which extends anteriorly as border. Portion of animal between valves and tube covered by thin, irregularly ridged periostracal sheath. Burrow opening often with small, white cone about 0.5 mm in diameter. Siphons short; incurrent siphon slightly longer than excurrent. Protoconch large, medium golden-brown and sculptured with fine, concentric ridges.

Valve measurements.

Length	Height	
2.5 mm	2.3 mm	Holotype
2.5	2.0	Paratype
2.1	2.0	"
2.0	1.9	"
1.5	1.4	"
1.5	1.2	"

Remarks. This species is most closely related to *Xyloredo naceli* from the eastern Pacific. It differs in having a less well-developed posterior slope, a shallow, indistinct umbonal-ventral groove, a flattened umbonal-ventral ridge, and in having the valves longer than high. In addition, the periostracal sheath posterior to the valves is not pustulose as in *naceli*, and the calcareous tube is much heavier and has raised rings. It also differs from *naceli* in having a much larger protoconch, which is sculptured with fine, concentric ridges.

It differs from *X. nooi* in having the valves longer than high, in having a low, rounded posterior slope, in lacking the distinct groove on the inner surface separating the disc from the posterior slope, and in having the plates of the mesoplax subrectangular and well calcified.

The wood dredged by the INGOLF Expedition had been heavily attacked by large teredinids before sinking to 1783 meters. These were all dead, only the empty tubes remaining as evidence of their presence. Filling every available space between the teredinid burrows were pipe-organ-like tubes of *Xyloredo* going both across and with the grain of the wood. Many of these tubes were 40 mm long and 1.2 mm in diameter. Jensen (1912: 56), in discussing the distribution of *Idas* [= *Idasola*] *argenteus* Jeffreys, states: "The specimens of the INGOLF Expedition were taken south of Iceland (61°30′N.L.; 22°30′W.L.) at 975 fathoms, under similar conditions to the last; the trawl brought up two large pieces of pine-wood, which had been pierced through and through by *Teredo*; in some of the *Teredo* tunnels were in addition mud and worm-tubes, further worms and small bivalves, namely *Idas argenteus*." This is the same piece of wood, remnants of which were preserved in the Copenhagen Museum, from which specimens of *Xyloredo ingolfia* were taken. The small, straight tubes were probably thought to be young teredinids.

The bottom at station 67 was a brown-gray transition clay of a fine, clayey-sandy consistency (Boeggild, 1900); the temperature was 3°C and the salinity 35.18 ‰ (M. Knudsen, 1899).

Range and specimens examined. Known only from the type locality.

Xyloredo naceli[1], new species

Plate 6

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[1] An acronym based on the initials of the Naval Civil Engineering Laboratory, Port Hueneme, California, which was responsible for the tests from which the specimens were obtained.

Type locality. From the U. S. Naval Civil Engineering Laboratory Submersible Test Unit at test site 1 [STU I–4], about 30 miles south of San Miguel Island, off Port Hueneme, California (33°46′N; 120°46′W), in 6800 feet [2072.6 meters], submerged from June 1964 to July 1965.

Types. Holotype, Museum of Comparative Zoology 279638. Paratypes from the same locality, Museum of Comparative Zoology 279639.

Description. Shell globose, valves reaching 1.5 mm in length and 1.5 mm in height, thin, fragile; umbos prominent. Periostracum thin, pale yellow, covering disc and posterior slope. Beaked portion of anterior slope with 8–12 pronounced, widely spaced, finely denticulated ridges. Posterior portion of anterior slope narrow; ridges extending to umbonal-ventral sulcus and more coarsely denticulated. Umbonal-ventral sulcus narrow, slightly depressed. Disc and posterior slope sculptured with fine growth lines only. Umbonal reflection narrow, free except at posterior end.

Inner surface of valves smooth and glistening. Umbonal-ventral ridge narrow and indistinctly segmented. Chondrophore and internal ligament well developed. Disc separated from posterior slope by low ridge. Posterior adductor muscle scar elliptical, extending from dorsal margin nearly to ventral margin and with indistinct, irregular, transverse markings. Pedal and siphonal retractor muscle scars impressed. Mesoplax of two small, thin, triangular plates composed almost entirely of periostracum.

Burrow six times length of valves; calcareous tubular lining two-thirds length of burrow, thin, marked with distinct rings, and covered with glistening, nearly colorless periostracum, which extends anteriorly as border. Portion of animal between valves and anterior end of calcareous tube with finely pustulose, light tan periostracal sheath. Siphons short, of about equal length and apparently lacking cirri. Protoconch very small, smooth (Plate 6, fig. 5).

Valve measurements.	Length	Height	
	1.1 mm	1.2 mm	Holotype
	1.5	1.5	Paratype
	1.2	1.3	"
	1.0	1.0	"

Remarks. This species, of which only eight small specimens were found, appears to be most closely related to *Xyloredo in-*

golfia from off Iceland. It differs by having a much smaller protoconch (hence the larvae in the pediveliger stage must be about two-thirds the size of those of *ingolfia*). It also differs in that the umbonal-ventral sulcus is impressed and the height of the valves is the same as or greater than the length.

The bottom at the test site was a green mud; the temperature was 2.1°C, the salinity 34.52 ‰, and the dissolved oxygen 1.26 ml/L (Muraoka, 1966b). This species has not been taken at test site II of the Naval Civil Engineering Laboratory, located north of San Miguel Island (34°06'N; 120°42'W), where the depth is 2340 feet [713.23 meters], the bottom temperature 7.2°C, the salinity 34.37 ‰, and the dissolved oxygen 0.42 ml/L (Muraoka, 1965). Specimens of *Xylophaga washingtona* Bartsch were found at both sites. It would appear that temperature and/or dissolved oxygen may be factor(s) controlling the distribution of *Xyloredo naceli*. However, so little is known about the biology of the Xylophagainae that no definite statements can be made at this time.

Range and specimens examined. Known only from the type locality.

ACKNOWLEDGMENTS

The author is grateful to John DePalma, U. S. Navy Oceanographic Office, Washington, D.C.; James Muraoka, U. S. Naval Civil Engineering Laboratory, Port Hueneme, California; and Dr. Jorgen Knudsen, Universitetets Zoologiske Museum, Copenhagen, Denmark, for the test panels and dredged wood from which the specimens were obtained. Thanks are also extended to Prof. Kenneth J. Boss of the Mollusk Department, Museum of Comparative Zoology, and Nancy Knowlton, my assistant, who critically read the manuscript. The aid granted by the Office of Naval Research through Contract no. N00014-67-A-0298-0027 with Harvard University is particularly appreciated.

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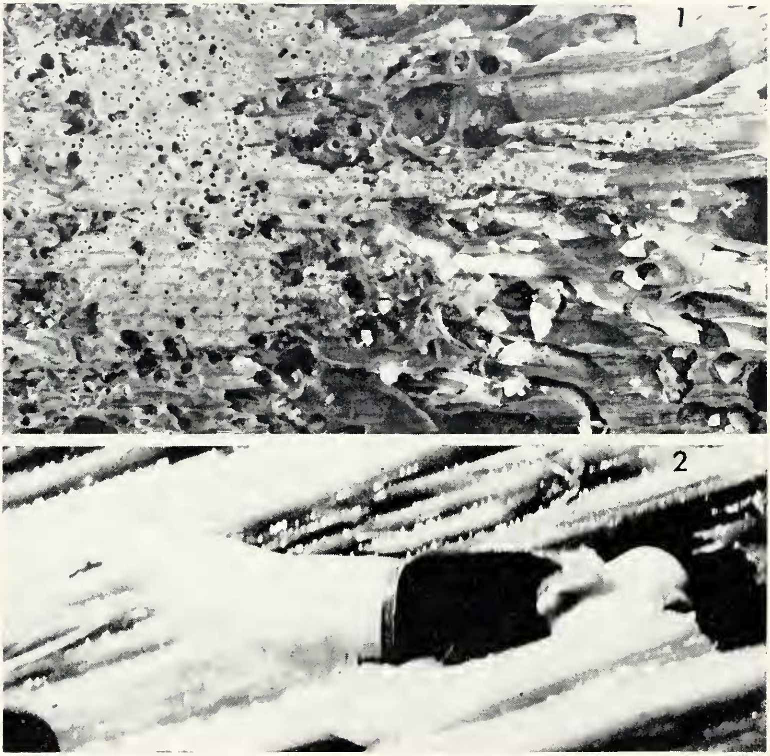


Plate 1

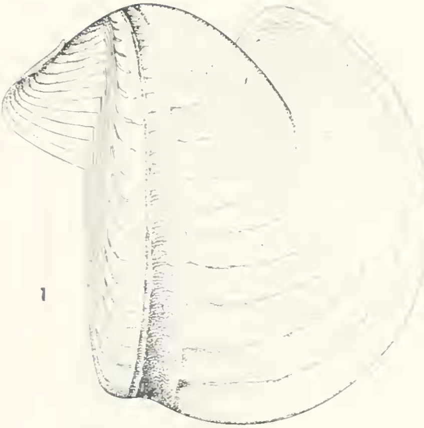
Xyloredo nooi Turner

Figure 1. Section of panel submerged in the Tongue of the Ocean, Bahama Islands, from April 4, 1962 to February 17, 1965 in 1737 meters (about 1/4 ×). Figure 2. Enlarged section of panel showing the calcareous lining of the burrow with anterior periostracal border, and dorsal view of apposed valves (about 4 ×).

Plate 2

Xyloredo nooi Turner

From panels submerged in the Tongue of the Ocean, off Andros Island, Bahama Islands. Figures 1–2. Holotype. Fig. 1. Outer view of left valve showing high, flaring posterior dorsal margin. Fig. 2. Inner view of right valve showing divided muscle scar, the deep groove separating the disc from the posterior slope, and the umbonal reflection. Figures 3–4. Outer and inner views of left valves of smaller specimens. Figure 5. Anterior view of apposed valves showing the chondrophore and internal ligament. Figure 6. Dorsal view of apposed valves showing mesoplax.



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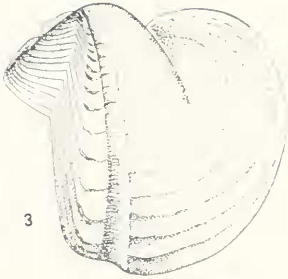

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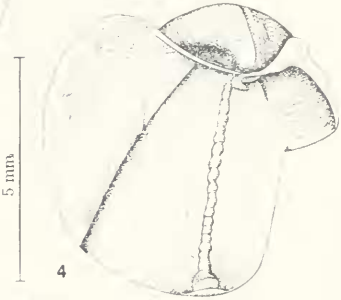

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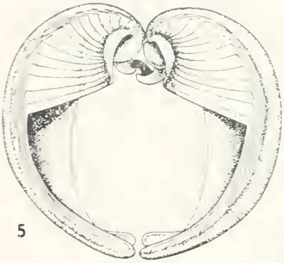

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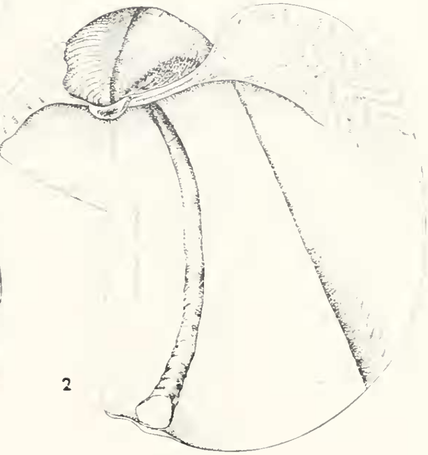

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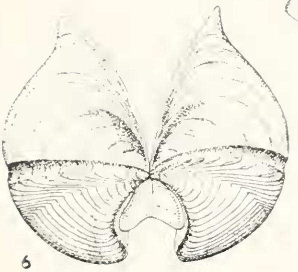

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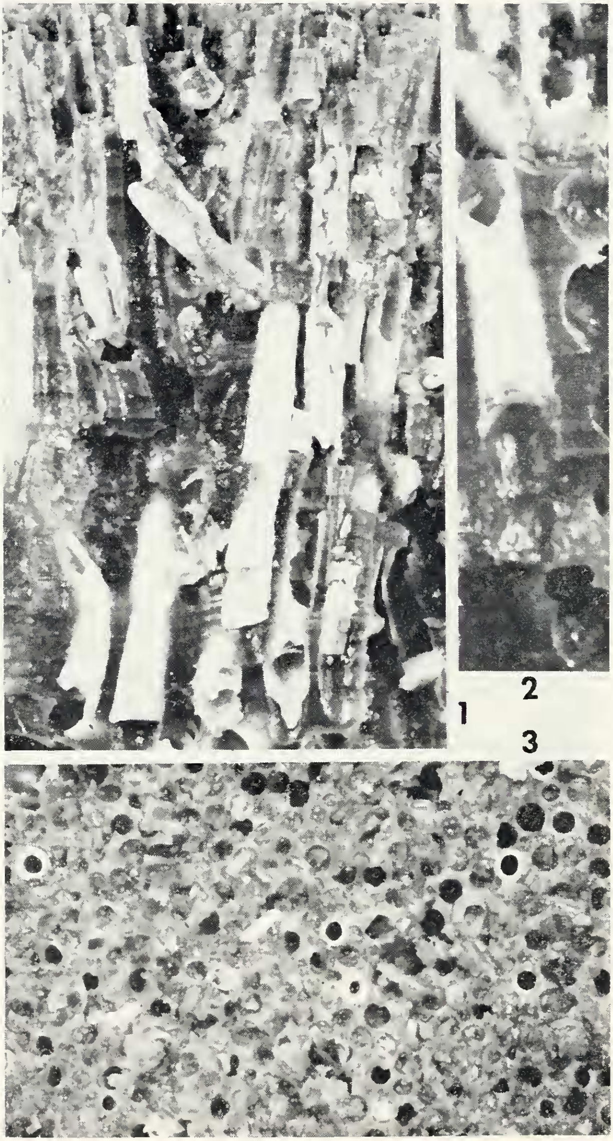

Plate 3

Xyloredo ingolfia Turner

Figure 1. Section through wood dredged at INGOLF-Expedition station 67, south of Eyrabakki, Iceland (61″30′N; 22°30′W) in 1783 meters, showing narrow, parallel tubes (5 ×). Figure 2. Enlarged section of burrow showing calcareous lining with anterior periostracal border (10 ×). Figure 3. Surface of wood showing entrances of burrows (5 ×).

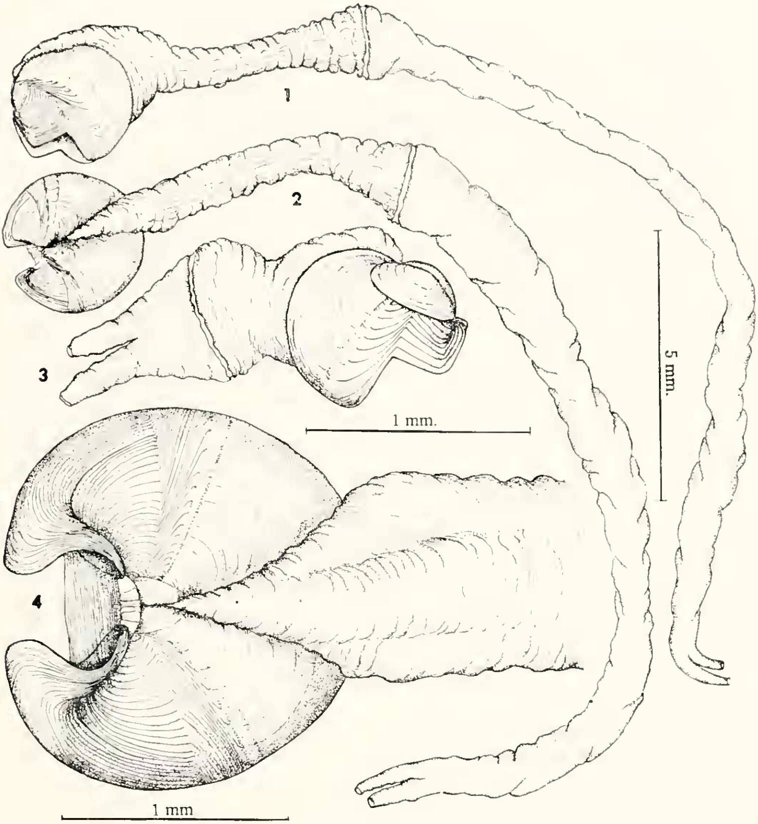

Plate 4

Xyloredo ingolfia Turner

From INGOLF-Expedition, station 67, south of Eyrabakki, Iceland.

Figures 1–2. (Holotype.) Lateral and dorsal views of entire animal showing the periostracal sheath, the extended anal and siphonal canals, and the short siphons. Figure 3. Lateral view of very young specimen showing large prodisoconch. Figure 4. Enlarged dorsal view of anterior end of entire specimen showing umbonal reflection, anterior adductor muscle, and small plates of the mesoplax in place.

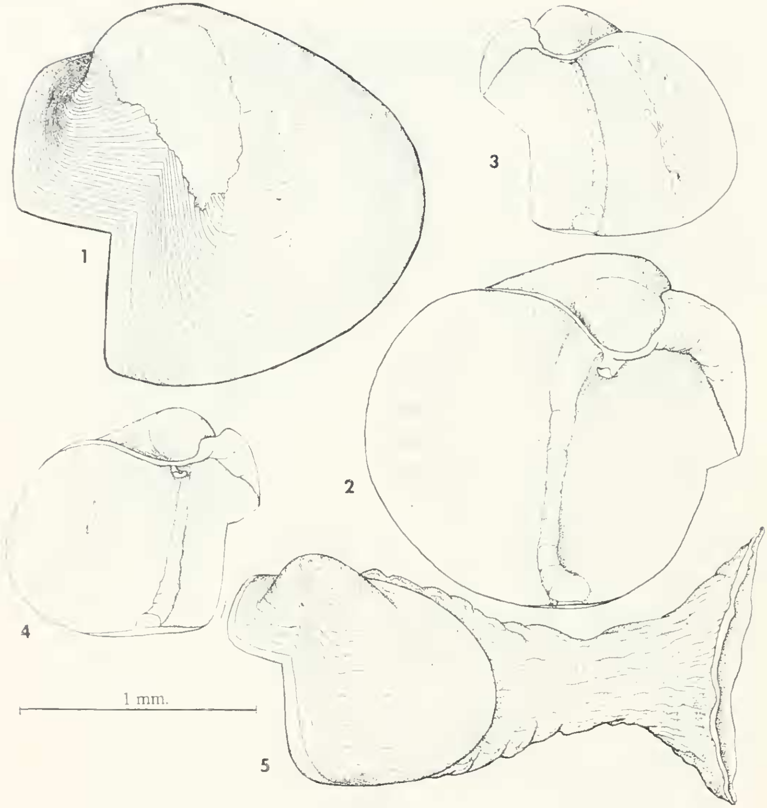

Plate 5

Xyloredo ingolfia Turner

From INGOLF-Expedition, station 67, south of Eyrabakki, Iceland.

Figure 1. Outer view of left valve showing wide anterior slope and low, rounded posterior slope. Figure 2. Inner view of left valve showing large prodisoconch, strong umbonal-ventral ridge, reduced posterior slope, and lightly impressed muscle scars. Figure 3. Inner view of right valve. Figure 4. Inner view of left valve. Figure 5. Outer view of left valve with periostracal sheath attached.

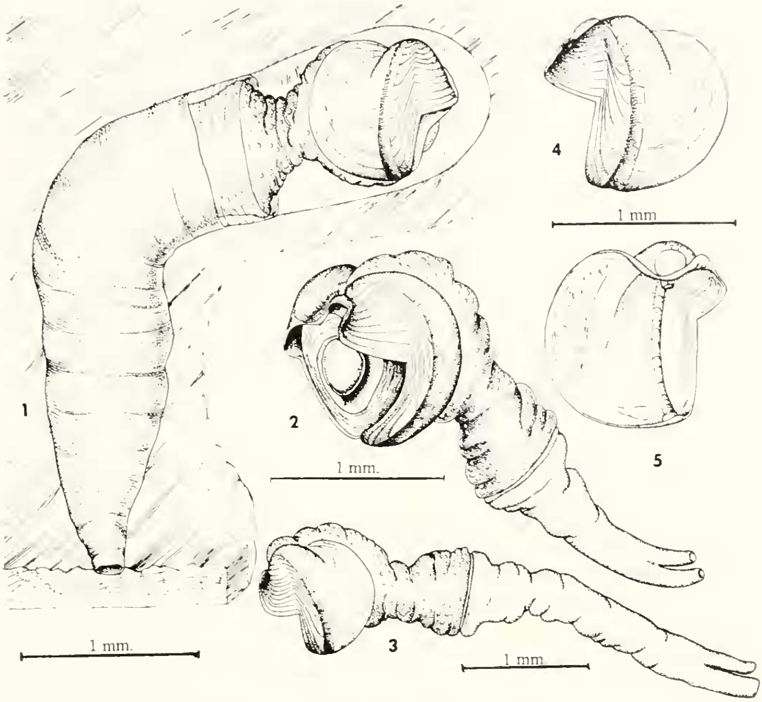

Plate 6

Xyloredo naceli Turner

From U. S. Naval Civil Engineering Laboratory test site I, south of San Miguel Island, Santa Barbara Islands, California.

Figure 1. Lateral view of specimen partially dissected from the wood showing the calcareous tube with the anterior periostracal margin and the papillose periostracal sheath covering the animal between the tube and the valves. Figure 2. Anterolateral view of entire specimen showing foot, mesoplax, and siphons. Figure 3. Lateral view of holotype. Figure 4. Outer view of left valve. Figure 5. Inner view of left valve showing muscle scars, chondrophore, umbonal-ventral ridge, and small prodisoconch.